PROC. ENTOMOL. SOC. WASH.
94(3), 1992, pp. 329–335

THE LIFE HISTORY AND IMMATURE STAGES OF A MARINE SHORE FLY, *HECAMEDE ALBICANS* (DIPTERA: EPHYDRIDAE)

B. A. Steinly

Illinois Natural History Survey, Center for Economic Entomology, 607 East Peabody Drive, Champaign, Illinois 61820 and Office of Agricultural Entomology, College of Agriculture, University of Illinois, 607 East Peabody Drive, Champaign, Illinois 61820.

Abstract.—The coastal marine habitat distribution and life cycle of *Hecamede albicans* (Diptera: Ephydridae) are described for the first time. In vitro, *H. albicans* completed development on putrefying *Mytilus edulis* (blue mussel) in 10–15 days. *Hecamede albicans* eggs are also described for the first time, and previous descriptions of the third-instar larva and puparium are augmented and/or modified. Differences in third-instar larval and puparial length ranges suggest that the quality and quantity of nutrient resources may affect morphometric parameters.

Key Words: *Hecamede albicans,* Ephydridae, life history

The Ephydridae (Diptera) are well represented in aquatic, semi-aquatic, and coastal marine habitats. The first in depth investigations of marine shore-fly ecology and distribution were completed in Scandinavia (Ardö 1957, Dahl 1959). Simpson (1976) reviewed the biology and distribution of Nearctic ephydrids that inhabit marine beaches and coastal marshes. Additionally, Barnby and Resh (1984) investigated the habitat distributions of adult shore flies within a California coastal marsh. Although the distributions of shore-fly adults from aquatic (Deonier 1965, Scheiring and Foote 1973, Deonier and Regensburg 1978b, Steinly and Deonier 1980, Steinly 1984, 1990, Steinly et al. 1987) and marine habitats (Dahl 1959, Barnby and Resh 1984, Steinly 1986) have been reported, less than 15% of ephydrid life histories and immature stages have been described from the Nearctic Region (Deonier and Regensburg 1978a, Zack 1983).

On the island of Guam, Bohart and Gressitt (1951) collected *Hecamede persimilis* Hendel third-instar larvae and puparia from a human cadaver that was washed up on a marine beach. Adults of *Hecamede persimilis* are common inhabitants of Hawaiian seashores, where they are found on decaying fish and crabs and have been reported developing in stranded marine seaweed (marine wrack) (Tenorio 1980). Both *H. persimilis* (Bohart and Gressitt 1951) and *H. albicans* (Meigen) (Norrbom 1983) have been reported associated with excrement. Adults of *H. albicans* have been collected in Scandinavian dune heath on dead herring (Ardö 1957), marine wrack, and the Hockenya (supralittoral) habitats (Dahl 1959). Although *H. albicans* has been reared on rotting lettuce (Simpson 1976), *Mytilus edulis* L. (blue mussel) (Steinly and Runyan 1979), and *Limulus polyphemus* L. (horseshoe crab) (Norrbom 1983), these reports did not exhaustively discuss life history characteristics.

This paper describes the life cycle and

coastal marine habitat distributions of *H. albicans*. Previous descriptions of the *H. albicans* third-instar larvae, puparium, and cephalopharyngeal skeleton (Norrbom 1983) are augmented and/or modified. Additionally, the discrepancies in third instar and puparia dimensions that were reported by Norrbom (1983) and compiled during this investigation are discussed.

Materials and Methods

Adults of *H. albicans* were collected at Anchor Beach, Milford, Connecticut. The marine beach was divided into distinct habitats that were characterized by plant and substrate types (Deonier 1979) and tidal effects (Neumann 1976). During submersion and emersion episodes, beach organisms are exposed to changing biological, chemical, and physical conditions. These conditions vary with intertidal range and are related to the magnitude of the tides. The supralittoral division of the intertidal zone (Neumann 1976) is flooded during storms and the marine tidal extremes of the equinoxes. The supra-midlittoral boundary is submerged biweekly by spring tides. The midlittoral is inundated by tides once or twice daily, and its sublittoral fringe is exposed only during the low waters of the spring tide. The land-to-sea dimensions of these intertidal divisions depend on the amplitude of the local tides and shore topography (Neumann 1976). Collecting was concentrated over marine wrack (supra-midlittoral boundary), midlittoral sand and rock, marine grass (sublittoral), and high sand beach (supralittoral) habitats.

Adults were collected with a modified aerial net (Regensburg 1977) or individually captured with a vial during June 1978 and 1979, and July and August of 1980 and 1981, respectively. Adults were aspirated from the aerial net, and single gravid females were transferred into 13 dram snap-cap vials (Plastic Container Corp.) that contained a freshly collected blue mussel. These oviposition vials were stored for 48 h in total darkness. After eclosion, individual first-instar larvae were isolated, and all stadia were exposed to a natural day/night cycle. In the absence of controlled laboratory conditions, rearing temperature fluctuated between 21° and 27°C. The morphological terminology of Teskey (1981) has been adopted to describe the immature stages.

Subsamples of eggs, larvae, and puparia were removed from the rearing vials and preserved in 80% ethanol. Additionally, viable and empty puparia were collected in the field from stranded decaying blue mussels, common spider crabs (*Libinia emarginata* Leach), and horseshoe crabs.

Larvae and pupae were dehydrated in an ethanol series before critical point drying in a Sandri 790 (Tousimis Research Corporation). Dried specimens were mounted on aluminum stubs with double-sided tape and sputter coated with gold-paladium (SPI Sputter). Specimens were coated twice at different angles to ensure complete coverage and to reduce charging effects. Life stages were examined with an Information Scientific Instrument DS-130 scanning electron microscope and photographed with Polaroid type 55 positive/negative film.

Life History

At Anchor Beach, adults of *H. albicans* were rarely collected over the supralittoral sand beach and rocks and sublittoral sand habitats. Although *Hydrellia griseola* (Fallén) was present on marine grass, and *Cirrula gigantea* Cresson, *Glenanthe litorea* Cresson, *Scatella favillacea* Loew, *S. obsoleta* Loew, and *S. paludum* (Meigen) were collected on algal encrusted rocks, *H. albicans* was not found within these sublittoral habitats during low tide. *Hecamede albicans* adults were collected over marine wrack rows and decaying marine animals that were located on the supralittoral-midlittoral boundary and in midlittoral sand beach habitats, respectively. Large numbers of adults were collected from decaying fish, spider crabs, horseshoe crabs, jelly fish, and

blue mussels that were stranded within the supralittoral and midlittoral habitat divisions. Adults were also routinely observed roosting in moist wrack rows but were not collected in marine marsh habitats near Anchor Beach.

Field observations and rearings confirm that *H. albicans* deposited eggs on the interior surfaces of decomposing spider crabs, blue mussels, and fish. After the limbs are broken, gravid females immediately enter the carcasses of horseshoe and spider crabs. *H. albicans* puparia were field-collected from horseshoe crab gill surfaces and empty blue mussel shells.

In total darkness, females deposited 5–14 eggs on the interior and exterior valve surfaces of blue mussels. Oviposition was completed in 48 h, and eggs hatched within 1–2 days. Comparable groups of gravid females subjected to a natural day/night cycle did not lay eggs.

Larval development on decaying blue mussels was completed in 8–13 days ($\bar{x}$ = 12 days). The duration of the first larval stadium was 1–2 days, the second 3–5 days, and the third 4–6 days. During development, *H. albicans* larvae moved through the liquid that was produced by the putrefaction of blue mussel tissue. Adults emerged in 1–2 days from puparia that adhered to the vial walls above the decomposing tissue. The developmental cycle of *H. albicans* was completed in 10–15 days. The capture of gravid females in June, July, and August and the short developmental cycle suggest that *H. albicans* is a multi-voltine species that produces more than 9 generations per year.

Description of Immature Stages

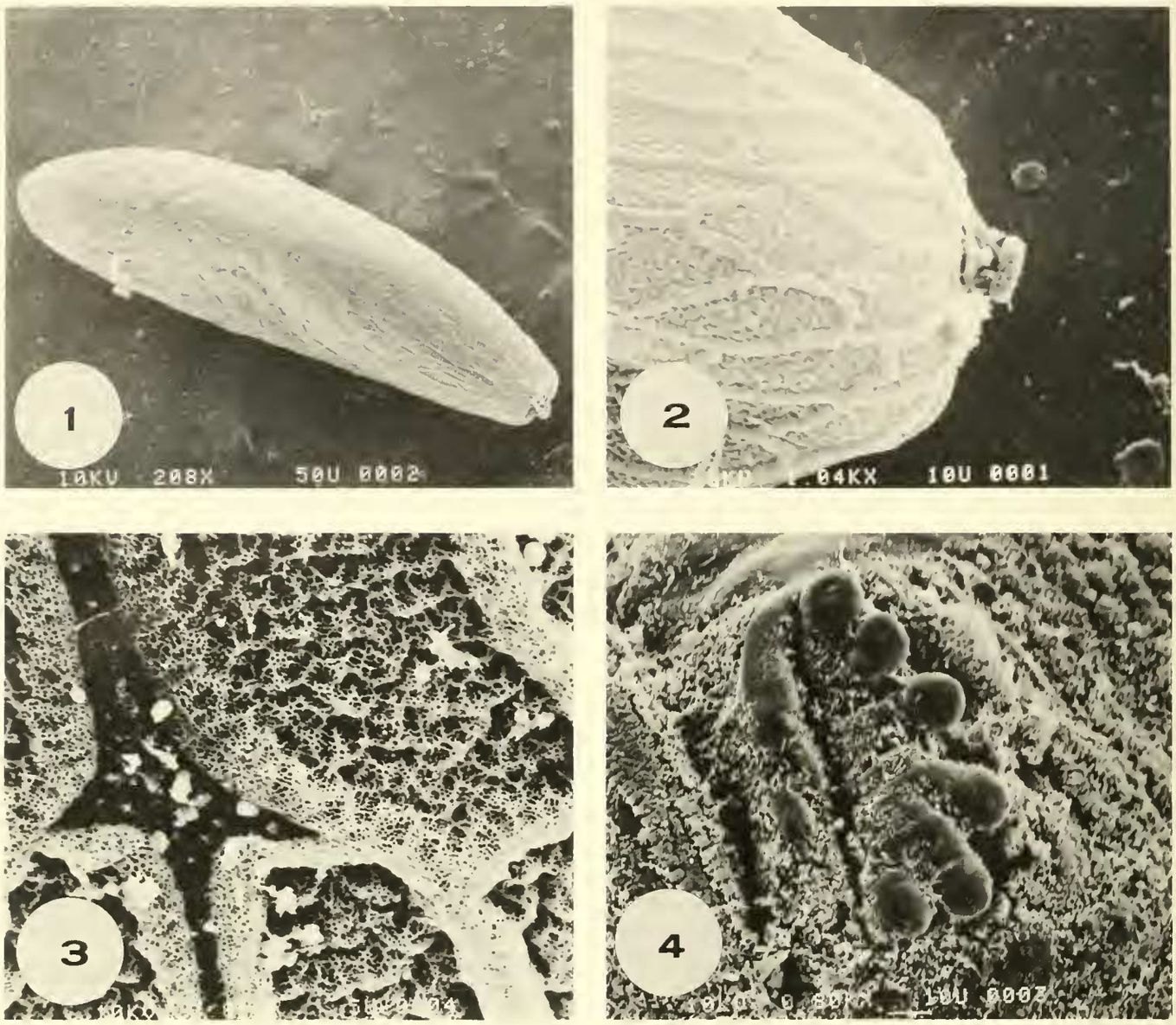
Eggs (Figs. 1–3).—Length 0.49–0.58 mm, $\bar{x}$ = 0.54 mm; width 0.14–0.20 mm, $\bar{x}$ = 0.17 mm (N = 16). Elliptical, slightly flattened ventrally; micropylar end truncate, opposite end bluntly rounded; micropylar disc with 0.012 mm diameter and 0.033 mm thickness, elevated 0.033 mm on a stalk (N = 2) (Fig. 2). Chorion opaque white, transparent at eclosion with distinctly irregular reticular pattern (Figs. 2, 3).

Mature third-instar larvae.—Length 3.89–5.28 mm, $\bar{x}$ = 4.60 mm; width 0.67–1.11 mm, $\bar{x}$ = 0.93 mm (N = 24). Cephalopharyngeal skeleton (CPS) ventral view 0.56–0.68 mm, $\bar{x}$ = 0.64 mm (N = 24). Anterior spiracles rounded apically with central opening (Fig. 4); 0.014 mm wide at base, slightly narrowed apically to 0.012 mm (Fig. 4). Antennae with 2 segments, basal segment ring-shaped (Fig. 5). Ventral surface with distinct creeping welts (Fig. 6). Posterior spiracle tube short, cylindrical with 3 spiracular openings, 4 sets of fine, multibranched hairs (Fig. 7). See Norrbom (1983) for additional description.

Puparium.—Length 2.70–3.24 mm, $\bar{x}$ = 2.94 mm; width 1.15–1.37 mm, $\bar{x}$ = 1.25 mm (N = 16). Posterior two-thirds of ventral surface flattened. Ten distinct segments, transverse sutures, ridges obvious. Segments 3–10 with lateral swelling. Anterior spiracles 6-lobed. Posterior spiracles short. Puparial emergence opening triangular with apex medially truncate, medial depression on truncate apex. See Norrbom (1983) for additional description.

Discussion

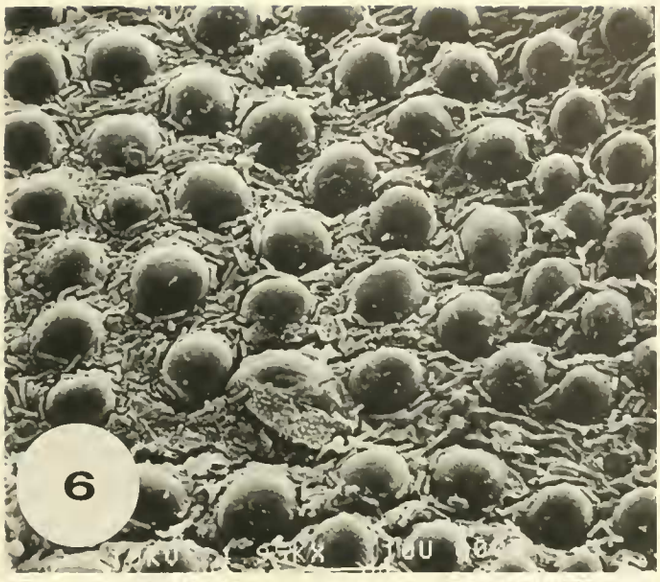
Scattered reports of *H. albicans* (Ardö 1957, Simpson 1976, Steinly and Runyan 1979, Norrbom 1983) and *H. persimilis* (Bohart and Gressitt 1951, Tenorio 1980) on decaying plant and animal remains substantiate the suggestion that these species are generalist scavengers on ephemeral nutrient resources. In the absence of wave action generated by storms, decaying nutrient resources and oviposition habitat in the supralittoral and midlittoral are infrequently inundated. Presumably, *H. albicans* avoids the disruption of ephemeral resources by storms and periodic tidal extremes of the equinoxes with a shortened developmental cycle (Steinly 1986). Shortened life cycles have been reported for *Scatella picea* (Walk-



Figs. 1–4. *Hecamede albicans*. 1, Egg. 2, Micropyle. 3, Areopyle. 4, Third-instar larva (anterior end).

er) and *S. stagnalis* (Fallén) (Diptera: Ephydridae) that commonly colonize freshwater ephemeral mud-shore habitats (Connell and Scheiring 1982, Foote 1979). In all probability, rapid shore-fly development, a temporal adaptation, allows these species to avoid dramatic increases of stream flow and/or wave action associated with storms (Steinly 1986).

Previously, a brief description of immature stages provided the basis for third-instar larvae and puparia identification (Norrbom 1983). Curiously, third-instar larvae and puparia found on decaying horseshoe crabs were smaller (Norrbom 1983) than individuals reared on blue mussels. Norrbom (1983) reported third-instar larvae, puparia, and CPS length ranges of 4.00–4.50 mm, 2.25–2.75 mm, and 0.65–0.70 mm, respectively, whereas third-instar larvae and puparia developing on putrefying blue mussels had length ranges of 3.89–5.28 mm ($\bar{x}$ = 4.60 mm, N = 24) and 2.70–3.24 mm ($\bar{x}$ = 2.94 mm, N = 16). Larvae raised on blue mussels had a CPS length range of 0.56–0.68 mm ($\bar{x}$ = 0.64 mm, N = 24). Although third-instar larval and puparia lengths from Anchor Beach specimens were different from Norrbom's (1983) descriptions and specimens, the life stage morphology and length



Figs. 5–7. *Hecamede albicans.* 5, Third-instar larva, antenna. 6, Third-instar larva creeping welts, ventral surface. 7, Third-instar larva posterior spiracle.

ranges of the CPS were similar. The differences in the length of the larvae and puparia suggest that a considerable amount of size variation exists within and between populations. The amount of CPS range overlap and a mean length within the range reported by Norrbom (1983) suggest that CPS development is less variable.

Variations in the length of *H. albicans* third-instar larvae and puparia may be the consequence of larval food quality, quantity, and availability. Previously, adult shore-fly size variation has been associated with feeding on different species of algae (Foote 1978, Zack and Foote 1978, Foote 1981a, b). These laboratory investigations suggest that the quantity and/or quality of nutrient resources may have a significant impact on larval survival and adult size.

Field examination confirmed that the putrefaction of dead horseshoe and spider crabs was a relatively slow process, whereas blue mussel tissues degenerated within 2 days in vitro. In the field, slow decomposition and the inaccessibility of crustacean viscera, competition, elevated temperature, and wind and solar desiccation may limit the optimal utilization of carrion resources during development. Norrbom (1983) reported that horseshoe crab viscera were dried or

consumed by unspecified muscid and calliphorid species in the field. In vitro, rapid degeneration of blue mussels assured that ample quantities of quality food were immediately available to emerging first instar *H. albicans* larvae. Additionally, *H. albicans* larvae were not competing with other dipterous species in vitro for limited nutrient resources, and they were not subjected to extreme physical and biological field conditions.

Acknowledgments

I am indebted to K. C. Kim for the loan of specimens from the Frost Entomological Museum at The Pennsylvania State University and to the Center for Electron Microscopy, University of Illinois, for technical assistance and access to the facilities. Additionally, I wish to thank Allen Norrbom, Systematics Entomology Laboratory, USDA, and Wayne Mathis, Smithsonian Institution, for suggestions regarding the direction of this investigation. May Berenbaum, Joel Siegel, and Donald Webb have provided constructive review of this manuscript. Finally, I wish to express my appreciation to Andra and Art Gumbus for sharing their home and invaluable knowledge of the Connecticut coast. Their hospitality and congenial companionship are greatly valued.

Literature Cited

Ardö, P. 1957. Studies in the marine shore dune ecosystem with special reference to the dipterous fauna. Opuscula Entomologica Supplementum XIV. Lund.

Barnby, M. A. and V. H. Resh. 1984. Distribution and seasonal abundance of brine flies (Diptera: Ephydridae) in a San Francisco Bay salt marsh. Pan-Pacific Entomologist 60(1): 37–46.

Bohart, G. E. and J. E. Gressitt. 1951. Filth-inhabiting flies of Guam. Bernice P. Bishop Museum, Bulletin 204: 1–152.

Connell, T. D. and J. F. Scheiring. 1982. Demography of the shore fly *Scatella picea* (Walker) (Diptera: Ephydridae). Environmental Entomology 11(3): 611–617.

Dahl, R. G. 1959. Studies on Scandinavian Ephydridae (Diptera, Brachycera). Opuscula Entomologica Supplementum XV. Lund.

Deonier, D. L. 1965. Ecological observations on Iowa shore flies (Diptera: Ephydridae). Proceedings of the Iowa Academy of Science 71: 496–510.

———. 1979. Introduction—a prospectus on research in Ephydridae, pp. 1–19. *In* Deonier, D. L., ed., First Symposium on the Systematics and Ecology of Ephydridae (Diptera). Oxford, Ohio: North American Benthological Society.

Deonier, D. L. and J. T. Regensburg. 1978a. Biology and immature stages of *Parydra quadrituberculata* (Diptera: Ephydridae). Annals of the Entomological Society of America 71(3): 341–353.

———. 1978b. New records of Ohio shore flies (Diptera: Ephydridae). Ohio Journal of Science 78(3): 154–155.

Foote, B. A. 1978. Utilization of blue-green algae by larvae of shore flies (Diptera: Ephydridae). Environmental Entomology 6(6): 812–814.

———. 1979. Utilization of algae by larvae of shore flies, pp. 61–71. *In* Deonier, D. L., ed., First Symposium on the Systematics and Ecology of Ephydridae (Diptera). Oxford, Ohio: North American Benthological Society.

———. 1981a. Biology and immature stages of *Lytogaster excavata*, a grazer of blue green algae (Diptera: Ephydridae). Proceedings of the Entomological Society of Washington 83(2): 304–315.

———. 1981b. Biology and immature stages of *Pelina truncatula*, a consumer of blue-green algae (Diptera: Ephydridae). Proceedings of the Entomological Society of Washington 83(4): 607–619.

Neumann, D. 1976. Adaptations of chironomids to intertidal environments, pp. 387–414. *In* Mittler, T. E., et al., eds., Annual Review of Entomology, Vol. 21, Palo Alto, California.

Norrbom, A. J. 1983. Four acalyptrate Diptera reared from dead horse shoe crabs. Entomological News 94(4): 117–121.

Regensburg, J. T. 1977. A modified sweep net for quantitative sampling. Entomological News 88(5&6): 141–142.

Scheiring, J. F. and B. A. Foote. 1973. Habitat distribution of the shore flies of northeastern Ohio (Diptera: Ephydridae). Ohio Journal of Science 73(3): 152–166.

Simpson, K. W. 1976. Chapter 17. Shore flies and brine flies (Diptera: Ephydridae), pp. 465–495. *In* Cheng, L., ed., Marine Insects. America Elsevier Publishing Company, New York.

Steinly, B. A. 1984. Shore fly (Diptera: Ephydridae) community structure in xeric grass habitat. Proceedings of the Entomological Society of Washington 86(4): 749–759.

———. 1986. Violent wave action and the exclusion of the Ephydridae (Diptera) from marine tempor-

ate intertidal and freshwater beach habitats. Proceedings of the Entomological Society of Washington 88(3): 427–437.

———. 1990. Shore-fly (Diptera: Ephydridae) community structure in selected terrestrial grass habitats of Ohio and Illinois. Proceedings of the Entomological Society of Washington 92(2): 188–193.

Steinly, B. A. and D. L. Deonier. 1980. New records of Ohio shore flies (Diptera: Ephydridae). Ohio Journal of Science 80(1): 41–42.

Steinly, B. A., E. A. Lisowski, and D. W. Webb. 1987. The distribution of shore flies (Diptera: Ephydridae) in Illinois. Entomological News 98(4): 165–170.

Steinly, B. A. and J. T. Runyan. 1979. The life history of *Leptopsilopa atrimana* (Diptera: Ephydridae), pp. 139–147. *In* Deonier, D. L., ed., First Symposium on the Systematics and Ecology of Ephydridae (Diptera). Oxford, Ohio: North American Benthological Society.

Tenorio, J. A. 1980. Family Ephydridae, shore flies, pp. 251–351. *In* Zimmerman, E. D., ed., Insects of Hawaii Vol. 13. Diptera: Cyclorrhapha III, by D. E. Hardy and M. D. Delfinado. University Press of Hawaii, Honolulu.

Teskey, H. J. 1981. Morphology and terminology—Larvae. 3 [chapter], pp. 65–88. *In* McAlpine, J. F. et al., eds., Manual of Nearctic Diptera. Vol. I. Monograph No. 27, 674 pp., Research Branch, Agriculture Canada.

Zack, R. 1983. Biology and immature stages of *Paracoenia bisetosa* (Coquillet) (Diptera: Ephydridae). Annals of the Entomological Society of America 76(3): 487–497.

Zack, R. and B. A. Foote. 1978. Utilization of algal monocultures by larvae of *Scatella stagnalis*. Environmental Entomology 7(4): 509–511.